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Neuroanatomy of the Common Dolphin (*Delphinus delphis*) as Revealed by Magnetic Resonance Imaging (MRI)

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KEYWORDS

common dolphin, neuroanatomy, magnetic resonance imaging, MRI, brain

ABSTRACT

In this study, magnetic resonance (MR) images of the brain of an adult common dolphin (*Delphinus delphis*) were acquired in the coronal plane at 66 antero-posterior levels. From these scans a computer-generated set of resectioned virtual images in orthogonal planes was constructed using the programs VoxelView and VoxelMath (Vital Images, Inc., Michigan State Univ.). Sections in all three planes reveal major neuroanatomical structures. These structures in the adult common dolphin brain are compared with those from a fetal common dolphin brain from a previously published study as well as with MR images of adult brains of other odontocetes. This study, like previous ones, demonstrates the utility of MR imaging (MRI) for comparative neuroanatomical investigations of dolphin brains.

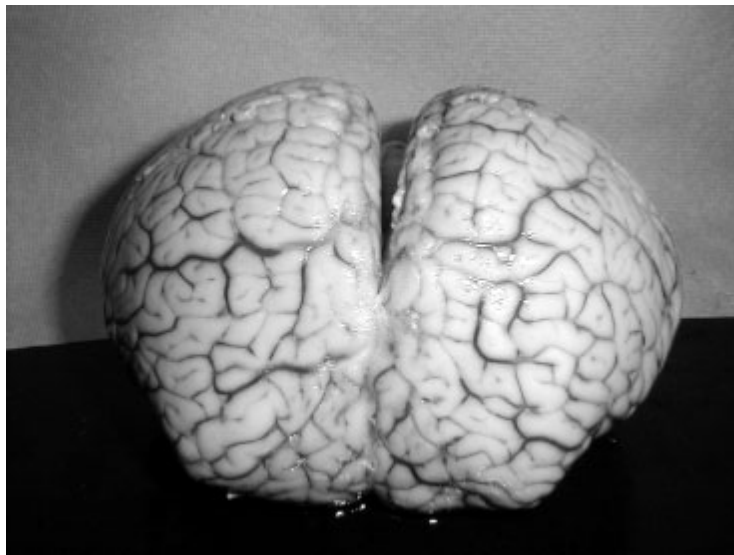
Compared with other mammalian brains, the cetacean brain is, in many respects, highly unusual. Morgane et al. (1980, p. 105) stated that “. . . the lobular formations in the dolphin brain are organized in a pattern fundamentally different from that seen in the brains of primates or carnivores.” As there is a 55–60 million year divergence between cetaceans and the phylogenetically closest group (the artiodactyls), odontocete brains represent a blend of early mammalian and uniquely derived features (Ridgway, 1986; Glezer et al., 1988; Ridgway, 1990; Manger et al., 1998). The differences between cetacean and other mammalian brains of similar size have been noted at the level of cortical cytoarchitecture and histochemistry (Garey et al., 1985; Garey and Leuba, 1986; Glezer and Morgane, 1990; Glezer et al., 1990, 1992a, b, 1993, 1998; Hof et al., 1992, 1995), cortical surface configuration (Jacobs et al., 1979; Morgane et al., 1980; Haug, 1987), and subcortical structural morphology (Tarpley and Ridgway, 1994; Glezer et al., 1995a, b). These differences are also manifest during ontogeny (Oelschlager and Buhl, 1985; Buhl and Oelschlager, 1988; Oelschlager and Kemp, 1998).

Although extensive studies have been conducted on the brains of other odontocetes, such as the bottlenose dolphin (*Tursiops truncatus*), there are very few published descriptions of the common dolphin brain. Existing studies, although quite valuable, have focused on either the volumetric and morphometric

properties of single brain structures or on regions such as the corpus callosum (Tarpley and Ridgway, 1994), brainstem (Hatschek and Schlesinger, 1902), and rhinencephalon (Addison, 1915), or whole-brain and body-weight ratios (Pilleri and Busnel, 1969; Marino, 1998). Those studies that do contain descriptions of several specific neuroanatomical features show very few brain sections (Pilleri and Gahr, 1970).

The one published description of the common dolphin brain that contains sequential neuroanatomical images in three orthogonal planes was conducted on a fetal common dolphin brain specimen using magnetic resonance imaging (MRI) (Marino et al., 2001a). Marino et al. (2001a) provides the basis for important comparisons with an adult specimen of the same species. Furthermore, MRI offers an opportunity to conduct more precise comparisons with sectioned and stained tissue because internal structures can be maintained, and thus can be analyzed in their precise anatomic positions. This is difficult to accomplish because of the spatial distortions that often accompany histological processing. Therefore, this work presents an anatomically-labeled three-dimensional (3D) description of the adult common dolphin brain from a series of MRI scans, and comparisons with a previously published description of a fetal specimen of the same species and the brains of other odontocete species.

Fig. 1. Photograph of the postmortem brain of the adult common dolphin.



MATERIALS AND METHODS

Specimen

The specimen (see Fig. 1 for a photograph) is the postmortem brain of an adult female, pregnant, common dolphin (*Delphinus delphis*) that stranded dead in February 2001 at Buxton, North Carolina (field #PTM135), with approximately seven other live common dolphins that eventually returned to the sea. The carcass was in fresh condition (Smithsonian Condition Code 2 (Geraci and Lounsbury, 1993)), with no evidence of damage. Total body length was 203 cm and total body weight was 83 kg. The brain was extracted from the skull approximately 24 hr after the dolphin was discovered. It was weighed and placed in 10% neutral buffered formalin 62 days prior to scanning. Fresh brain weight was 981 g. The specimen measured 132 in anterior–posterior length, 155 cm in bitemporal width, and 96 mm in height.

MRI

MR images of the entire brain were acquired in the coronal plane (cross-sectional to the major axis of the brain) at 66 antero-posterior levels with a 1.5 T Philips NT scanner (Philips Medical System, The Netherlands) at Emory University School of Medicine. Protocol parameters were: slice thickness = 2.0 mm, slice interval = 0 mm, time to repetition = 3000 msec, time to echo = 13 msec, number of signals averaged = 2, field of view = 180 mm, matrix = 256 = 256 pixels.

3D Reconstruction and Reformatting

Computer-generated 3D reconstruction images were created using the software programs VoxelView and VoxelMath programs (Vital Images, Inc.) at the Laser Scanning Microscopy Laboratory at Michigan State University. The 3D-rendered model was then digitally resectioned in orthogonal planes to produce corresponding virtual-section series in the horizontal (197 0.5-mm-thick virtual sections) and sagittal (223 0.7-mm-thick virtual sections) planes.

Anatomical Labeling and Nomenclature

All identifiable anatomical structures of the dolphin brain were labeled in the originally-acquired coronal plane images as well as in the images from the virtual-sectioned brain in the sagittal and horizontal planes. The nomenclature used is from Morgane et al. (1980). The MR images of the dolphin brain were compared with the published photographs and illustrations of the bottlenose dolphin brain from Morgane et al. (1980) as well as with published neuroanatomical atlases based on MRI scans of adult bottlenose dolphin and beluga whale brains (Marino et al., 2001b, c). All scans were also compared with a complete alternate series of sections of bottlenose dolphin brains stained, respectively, for cell bodies (Nissl method), and for myelinated fibers in the same three orthogonal planes. These stained section series are from the Yakovlev-Haleem collection at the National Museum of Health and Medicine, and the Welker collection at the University of Wisconsin–Madison.

Volumetric Estimate of Whole-Brain Weight

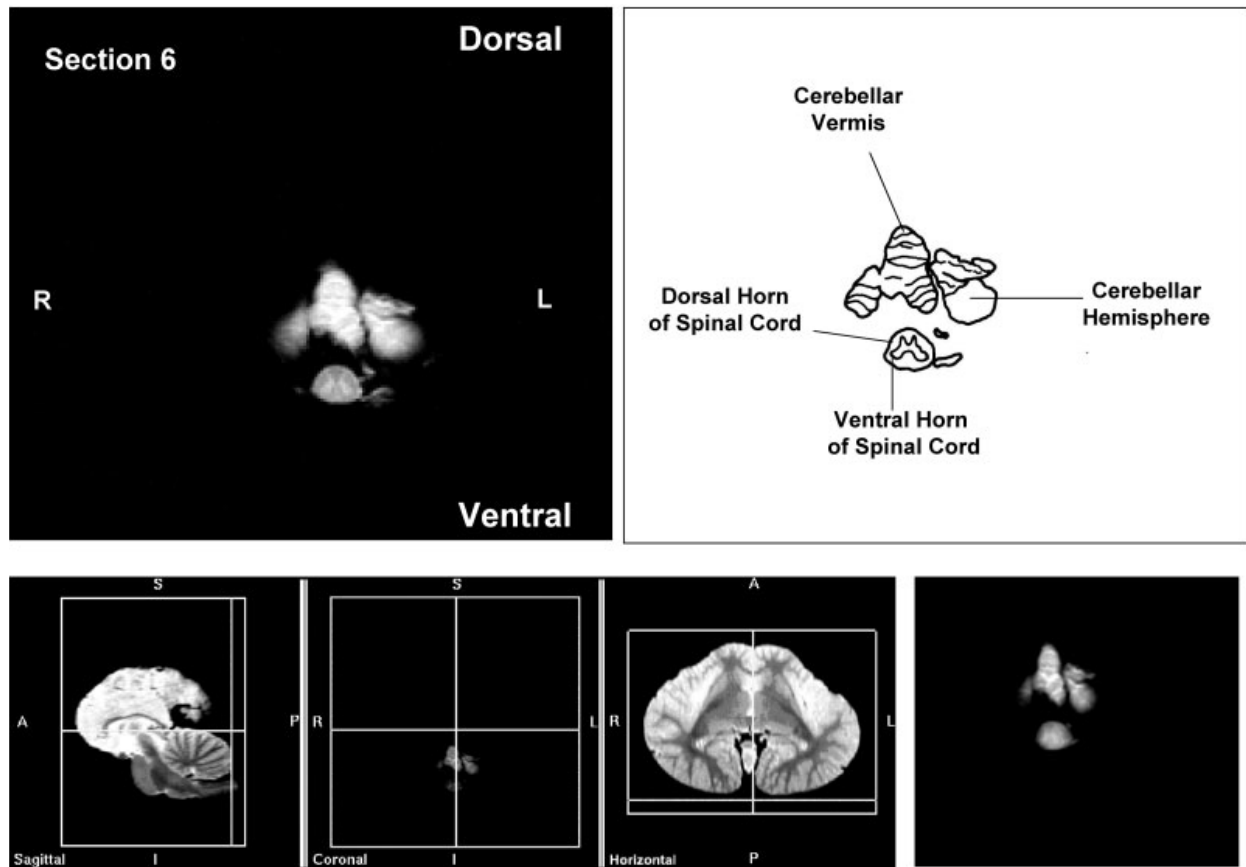
The full antero-posterior extent of the brain in coronal sections was measured with the image analysis software program Scion IMAGE for Windows (PC version of NIH IMAGE) using manually-defined areas from successive slices that are integrated to arrive at a volume estimate. The entire volumetric estimate was converted to weight units by multiplying the volume by the specific gravity of brain tissue or 1.036 g/cm^3 (Stephan et al., 1981).

RESULTS

Volumetric Estimate of Whole-Brain Weight

The measured whole-brain volume based on MRI was 990.34 cc. When converted to weight by multiplication with the value of the specific gravity of water, the estimate of whole-brain weight from the MR images was $1,025.99 \text{ g/cm}^3$. This estimate is only 4% more than the fresh brain weight of 981 g. Additionally, a previously published value for average cranial capacity in adult common dolphins was 815. cc (Marino, 1998). Pilleri and Busnel (1969) published a fresh brain weight of 805.1 g for adult common dolphins. However, the present specimen was substantially larger in both body length and weight than the specimens in either Marino (1998) or Pilleri and Busnel (1969).

Figs. 2–10. A posterior–anterior sequence of originally-acquired 2.0-mm-thick coronal MR brain sections at 12-mm intervals, a labeled schematic illustration of each section, computer-generated cutaways shown at two orthogonal planes to the section, and a computer-generated 3D reconstruction of the whole brain showing a cutaway of each section.



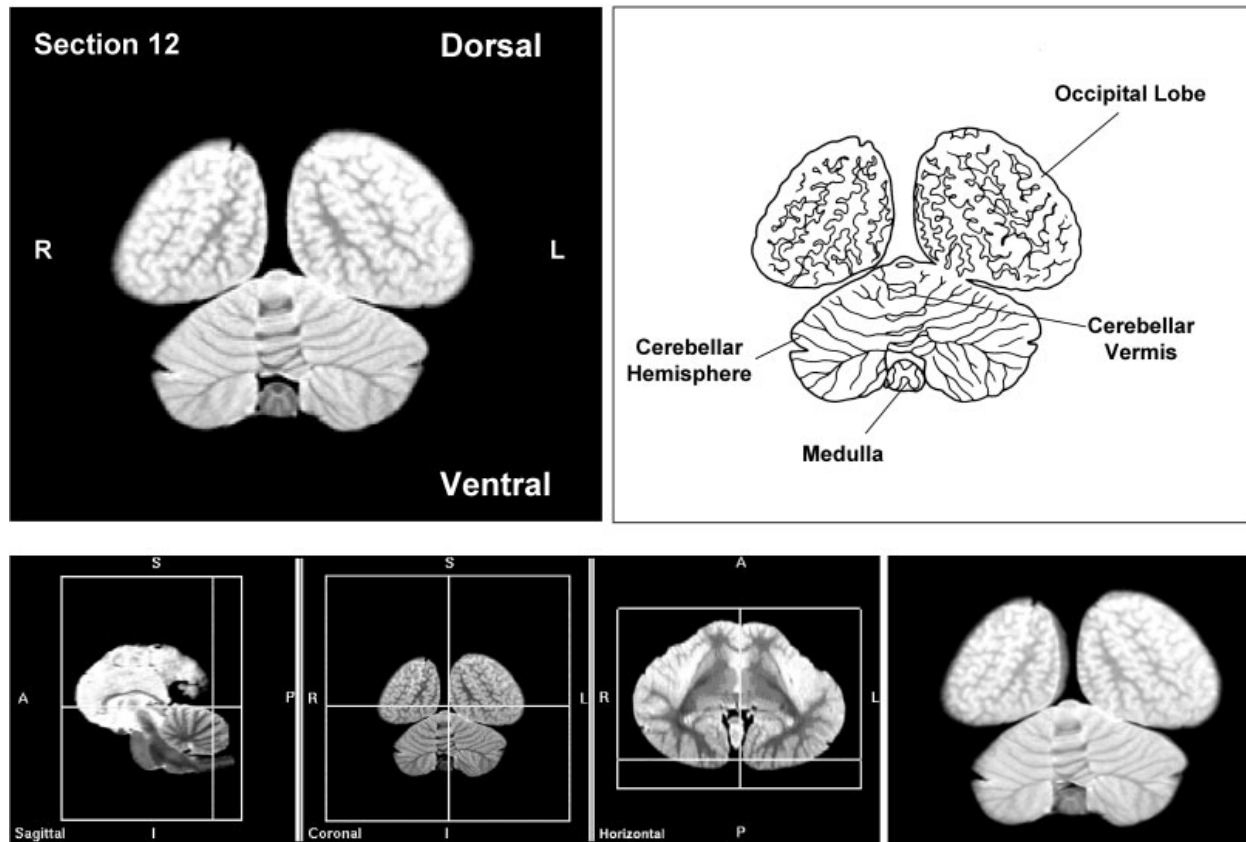
Anatomical Description

Figures 2–10 display a posterior–anterior sequence of originally-acquired 2.0-mm-thick coronal MR brain sections at 12-mm intervals, a labeled schematic illustration of each section, computer-generated cutaways shown at two orthogonal planes to the section, and a computer-generated 3D reconstruction of the whole brain showing a cutaway of each section. Figures 11–19 display a ventral–dorsal sequence of reconstructed “virtual” 0.5-mm-thick horizontal sections at 10-mm intervals, a labeled schematic illustration of each section, computer-generated cutaways at two orthogonal planes to the section, and a computer-generated 3D reconstruction of the whole brain showing a cutaway of each section. Figures 20–28 display a midline–lateral sequence of reconstructed 0.7-mm-thick “virtual” sagittal sections through the left hemisphere at 5.6-mm intervals, a labeled schematic illustration of each section, computer-generated cutaways of two orthogonal planes to the section, and a computer-generated 3D reconstruction of the whole brain showing a cutaway of each section.

Figures 2–10 reveal the exceptional level of preservation of the spatial relationships among the brain's structures that allowed for reconstruction in the horizontal and sagittal planes shown in Figures 11–19 and 20–28, respectively. Figures 20 and 21 show the mesencephalic and pontine flexures reminiscent of

brainstem flexure patterns in the embryonic state of most terrestrial mammals. These flexures remain present in adult dolphin brains and may represent pedomorphic features.

Figure 3



One of the features of the brain that is apparent in the photograph (Fig. 1) but is not replicated well in the 3D reconstructions is the great degree of cortical convolution. However, cortical convolutions are clear in several of the sections, including Figures 3, 4, 18, and 19, and all of the sagittal sections. The extreme depth and density of cortical sulci are particularly evident in Figures 24 and 25. The occipital-parietal elaboration characteristic of the current specimen and other dolphin brains is evident in Figures 23 and 24 in the three-tiered arrangement of limbic, paralimbic, and supralimbic arcuate cortical lobules divided by the deep limbic and paralimbic clefts. This specific combination of occipital-parietal organization and elaboration is distinct from other noncetacean mammals but is not unique to the common dolphin among the cetaceans (Morgane et al., 1980; Marino et al., 2001b). The common dolphin brain is very different from other noncetacean, mammalian brains at the cortical level, but generally resembles other mammalian brains on a subcortical level (Morgane et al., 1980). The subcortical differences between the common dolphin brain and other noncetacean mammalian brains are typically those of proportions of various structures. However, there are also differences in spatial arrangement of fiber systems and structures. For instance, the cerebral peduncle is located high on the lateral surface of the ventral midbrain (see Fig. 7). In most other mammals the cerebral peduncle wraps around the ventral surface of the midbrain. The lateral configuration of the cerebral peduncle is also found in other odontocete brains.

The adult common dolphin brain is very similar, at least at the gross morphological level, to that of the adult bottlenose dolphin brain (Marino et al., 2001b). There is a great resemblance between the cortical surface features of the common dolphin brain and the bottlenose dolphin brain. Furthermore, although a

comprehensive comparative analysis of sulcal and gyral formations between the bottlenose and common dolphin remains to be conducted, it appears that there is substantial similarity at the level of the location and morphology of cortical gyri and sulci. Also, at the subcortical level the proportions of most of the structures appear to be similar across the two species. As in other cetacean brains, olfactory structures are absent and auditory structures, such as the inferior colliculus, are proportionately very large (see Figs. 6, 15, 22, and 23) in the common dolphin brain. Just as in the bottlenose dolphin brain, the enlargement of auditory processing structures in the common dolphin brain is not accompanied by reduced visual structures. Consistent with the behavioral and electrophysiological evidence for a high degree of hemispheric independence (Viamonte et al., 1968; Mukhametov et al., 1977; Mukhametov, 1984), the corpus callosum is small relative to the massive hemispheres. This finding is also consistent with quantitative evidence in other odontocete species and observations of the bottlenose dolphin and beluga whale brain (Marino et al., 2001b, c; Tarpley and Ridgway, 1994). This feature is most evident in Figures 20–23. Just as in the bottlenose dolphin and beluga brain, the cerebellum in the common dolphin brain is large relative to the hemispheres. This is particularly evident in Figures 3–6 in the coronal plane and Figures 20–24 in the sagittal plane. Furthermore, the morphology of the cerebellum, at least at the gross level, appears similar to that of the bottlenose dolphin. Additional features of the common dolphin brain that are characteristic of cetaceans in general include a large thalamus (particularly evident in Figs. 23 and 24), a large pontine area (Figs. 20–22), and a reduced hippocampal region (which should be prominent but is not in Fig. 8).

Figure 4

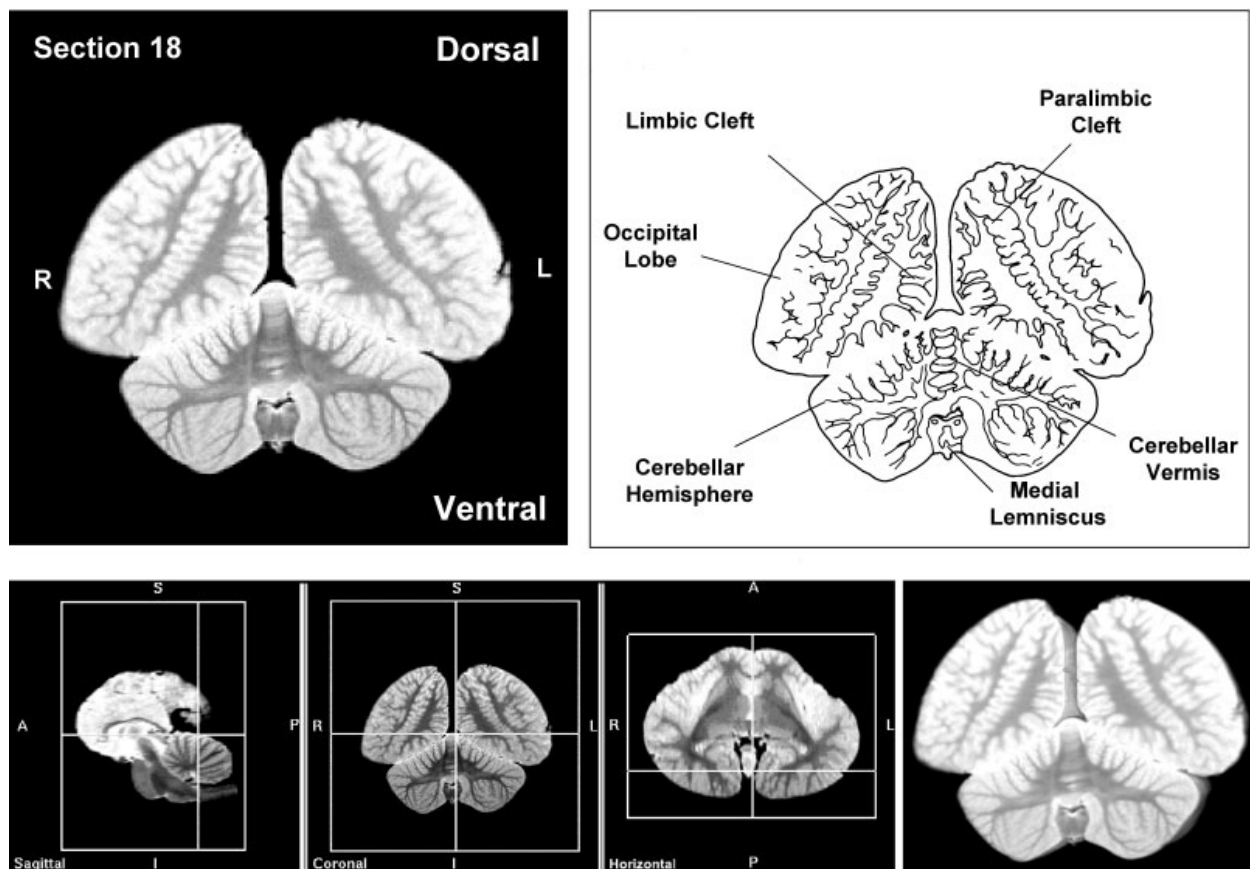


Figure 5

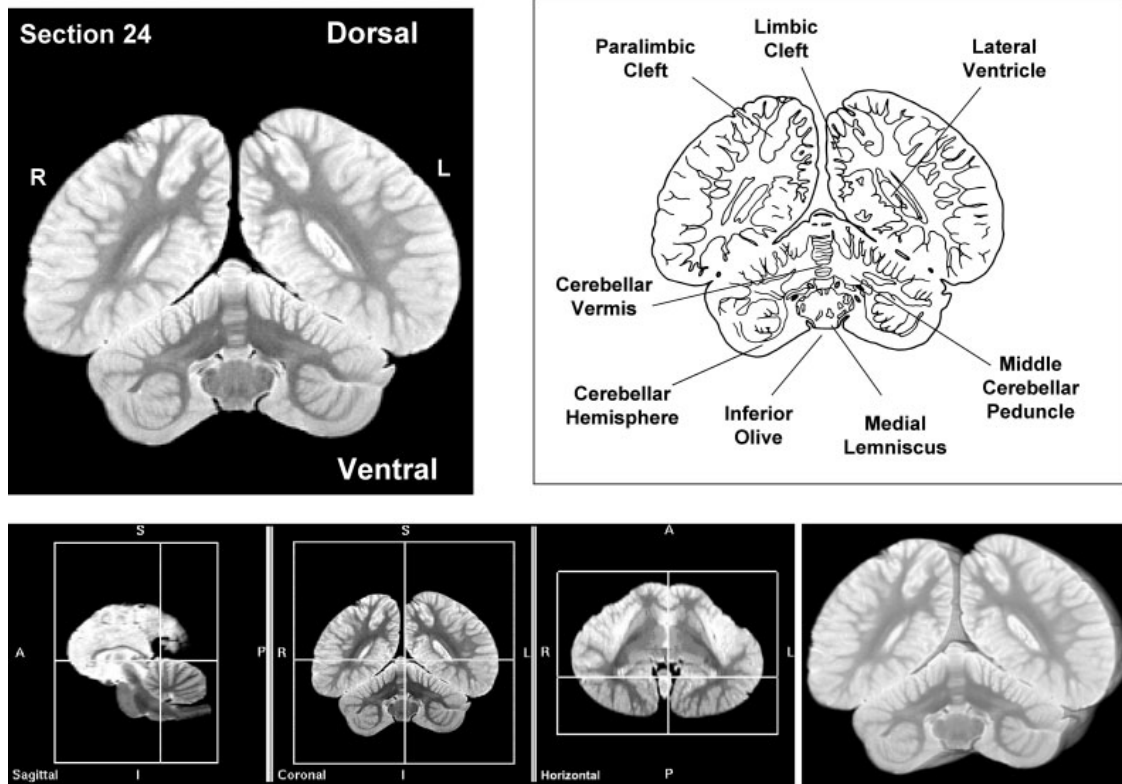


Figure 6

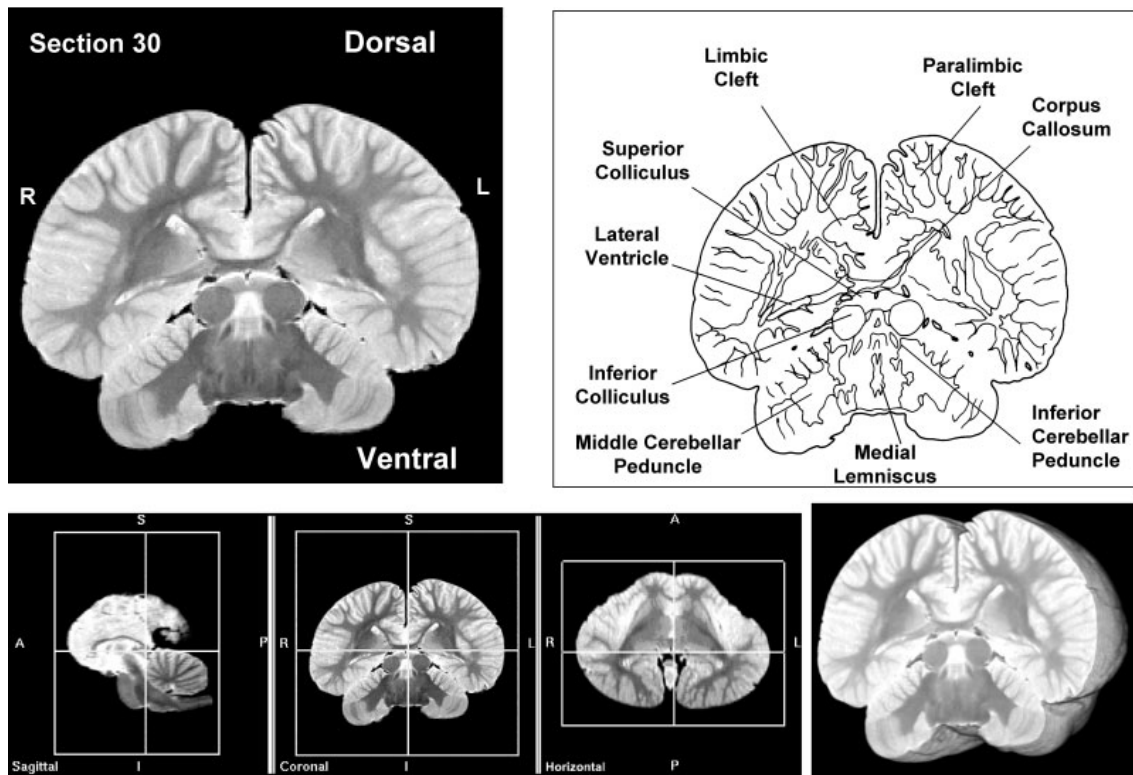


Figure 7

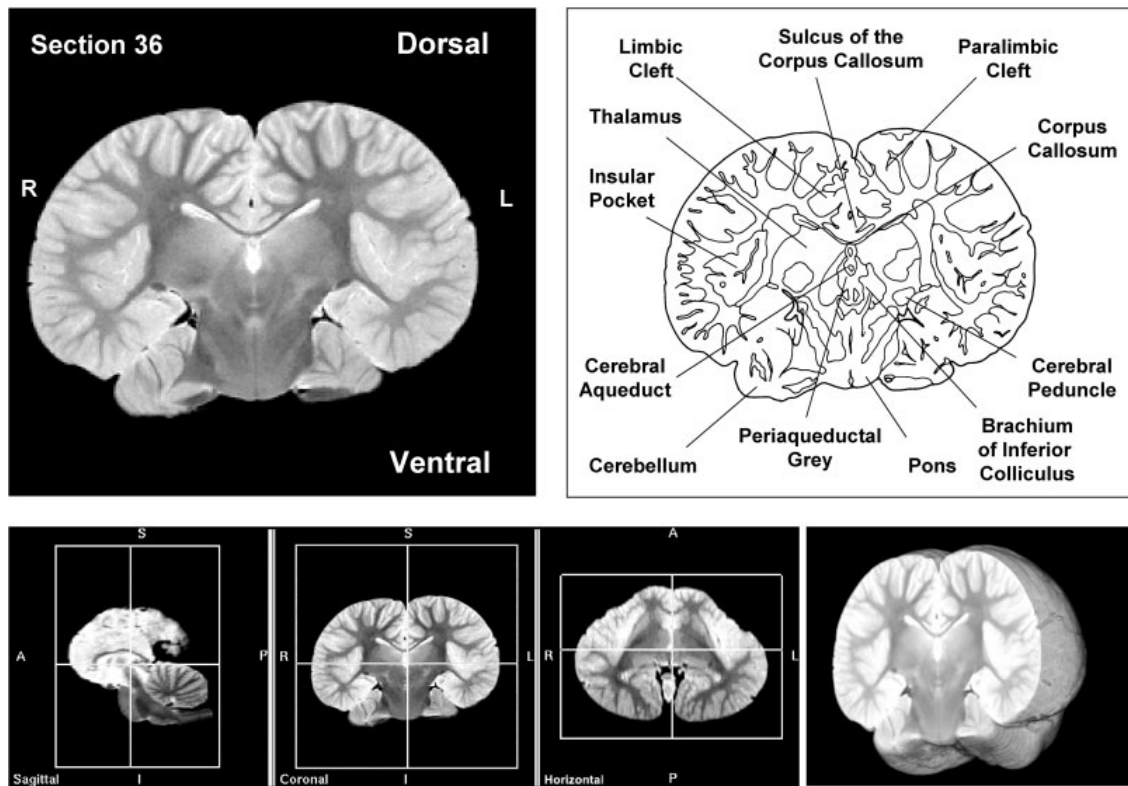


Figure 8

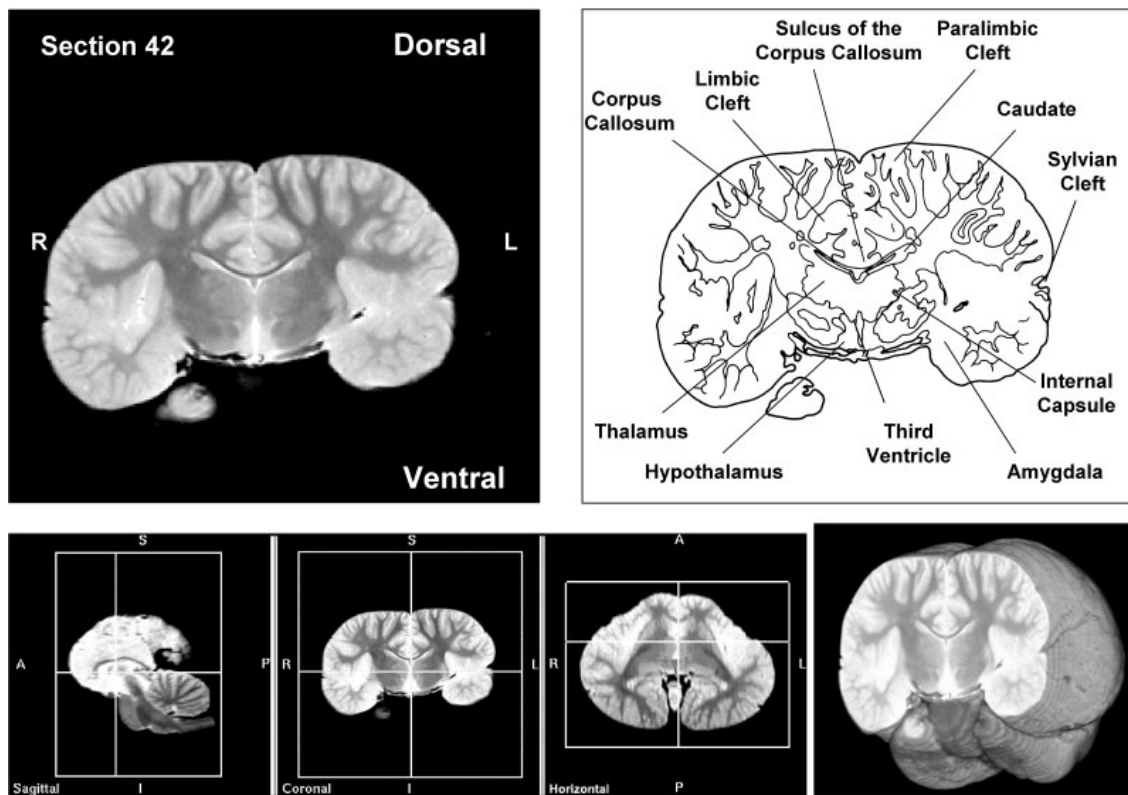


Figure 9

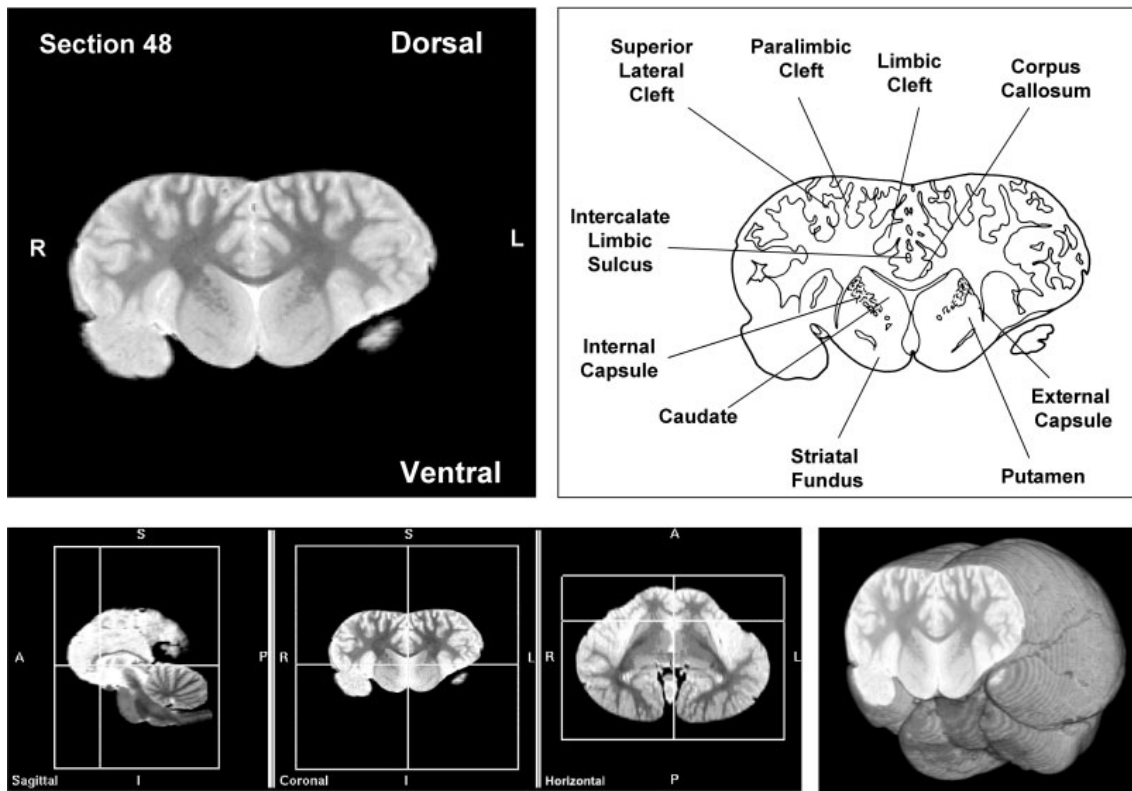
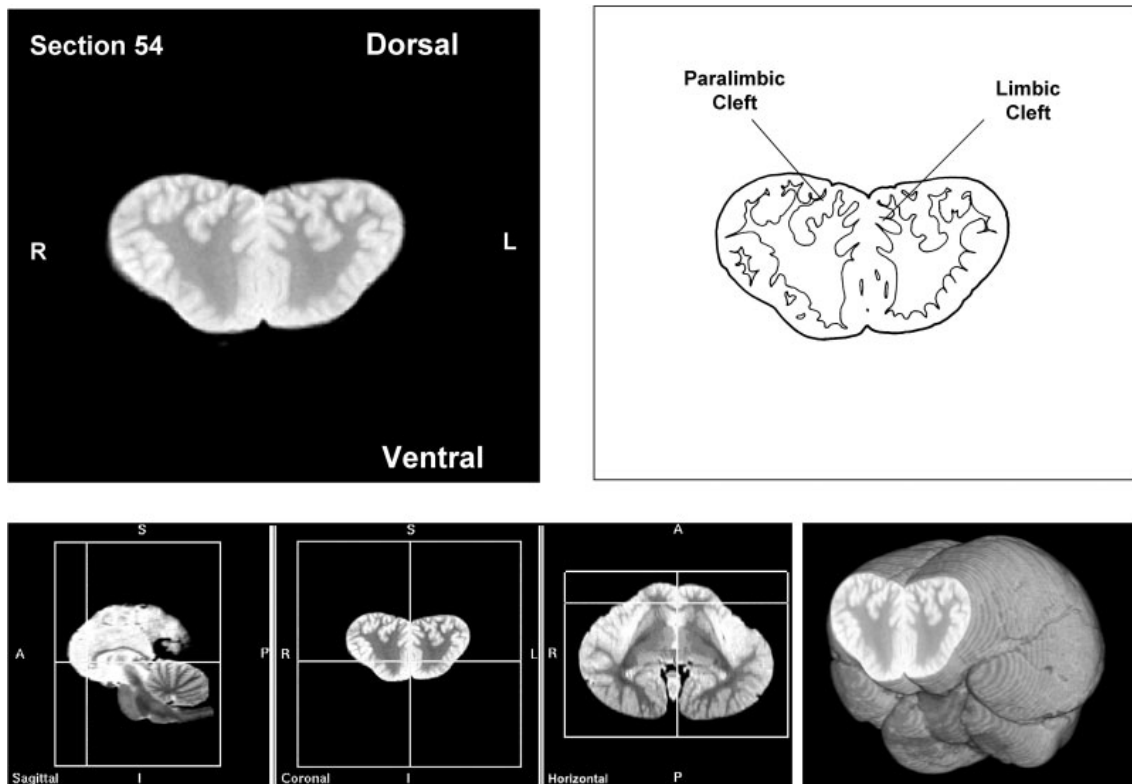


Figure 10



Figures 11–19. A ventral–dorsal sequence of reconstructed “virtual” 0.5-mm-thick horizontal sections at 10-mm intervals, a labeled schematic illustration of each section, computer-generated cutaways at two orthogonal planes to the section, and a computer-generated 3D reconstruction of the whole brain showing a cutaway of each section.

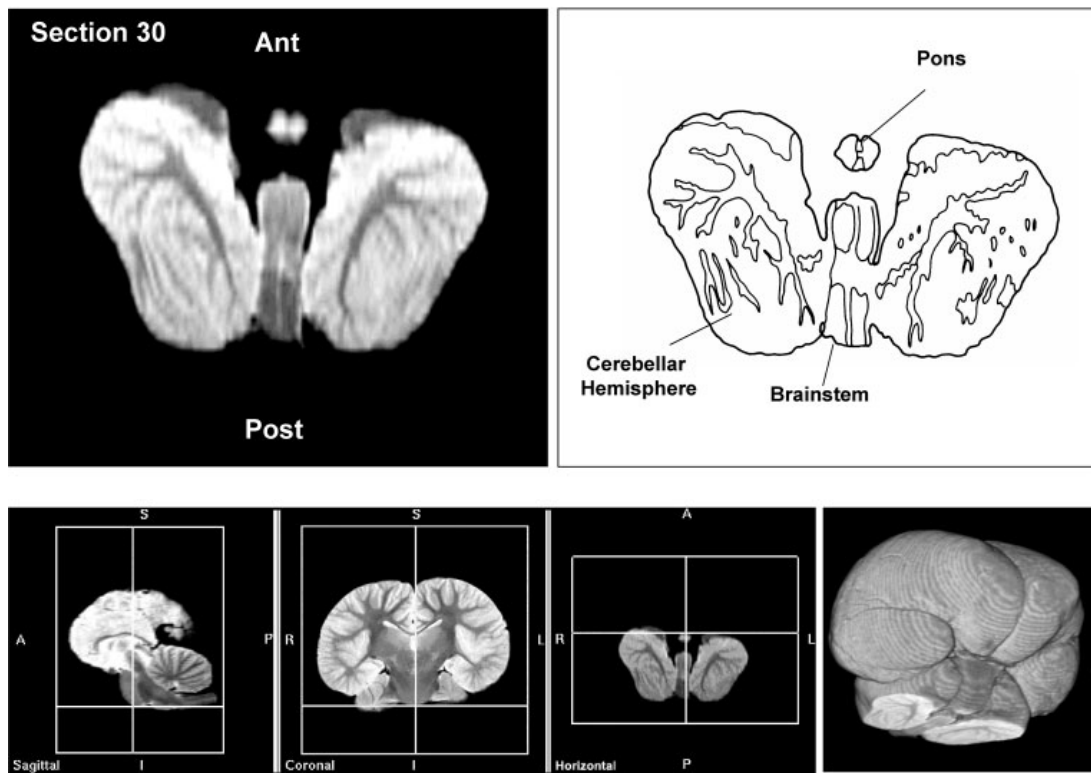


Figure 12

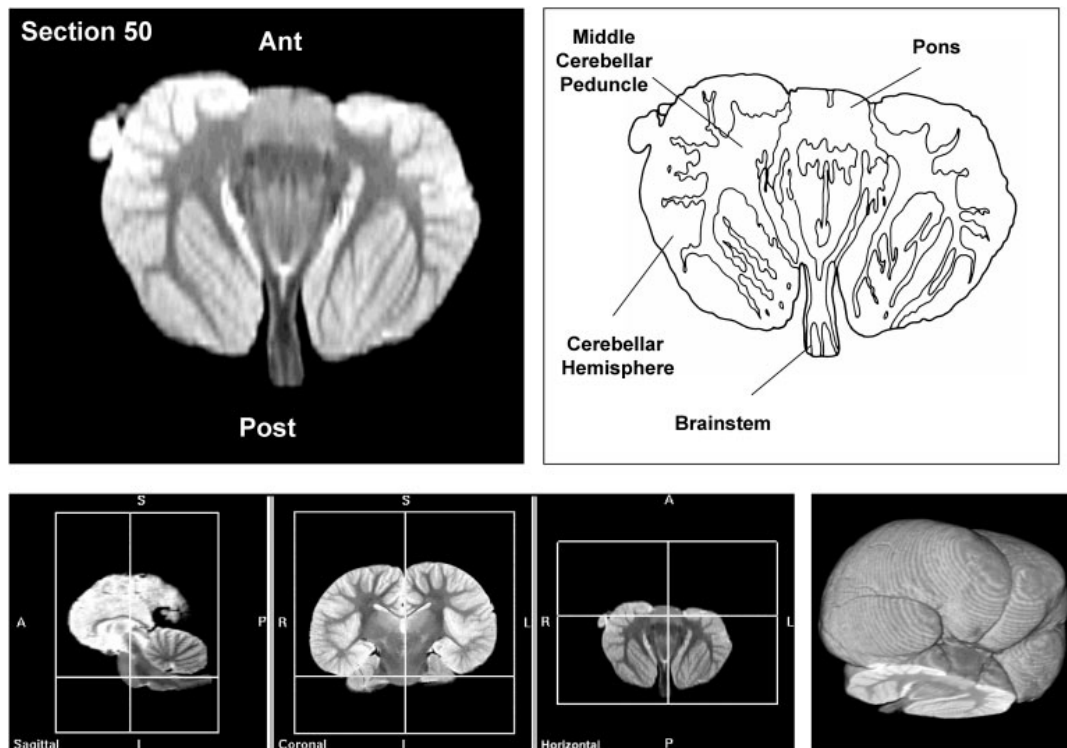


Figure 13

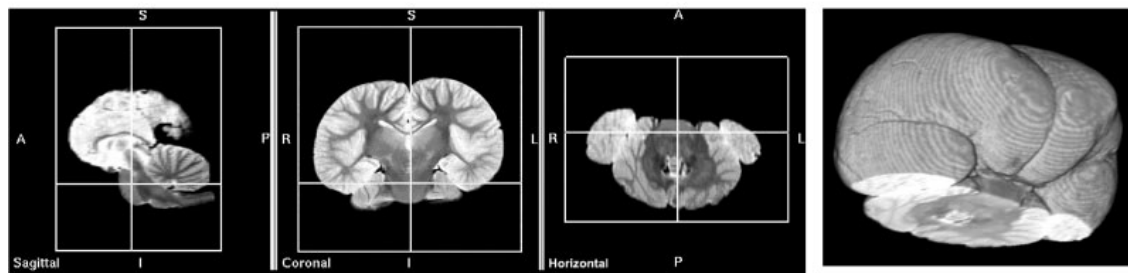
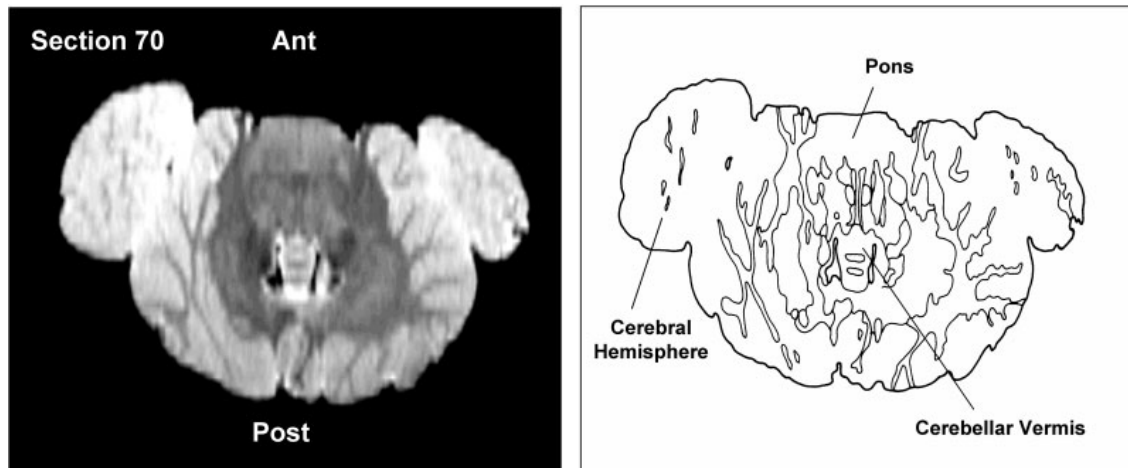


Figure 14

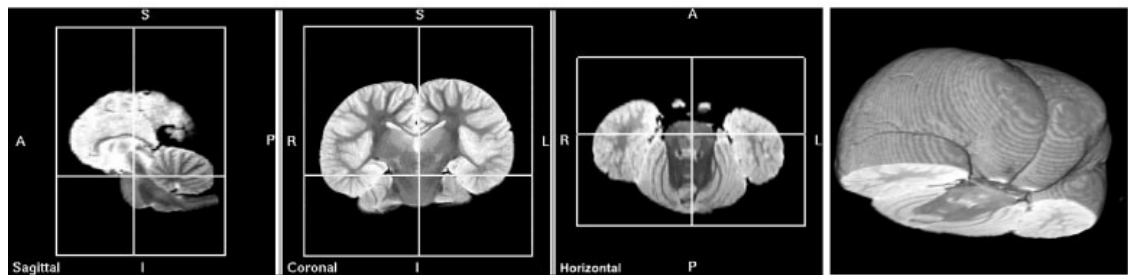
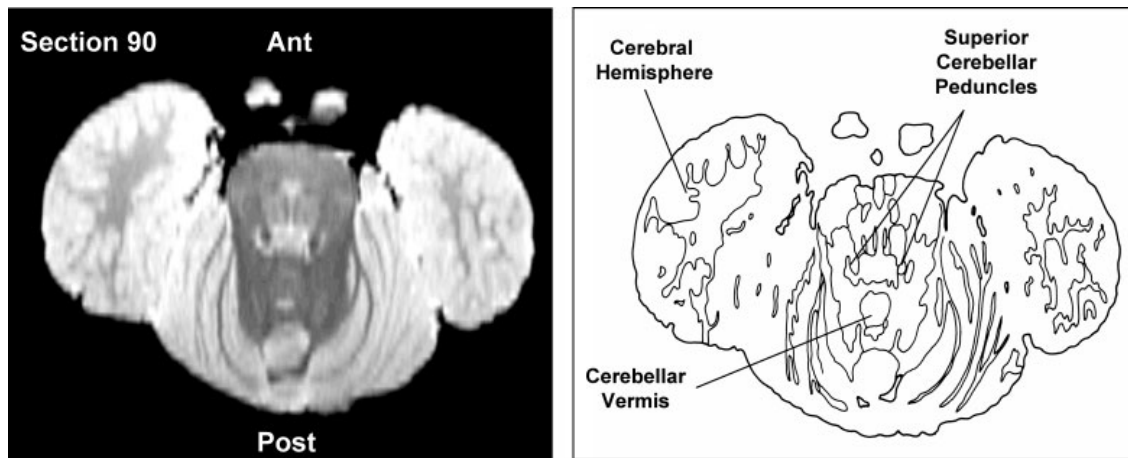


Figure 15

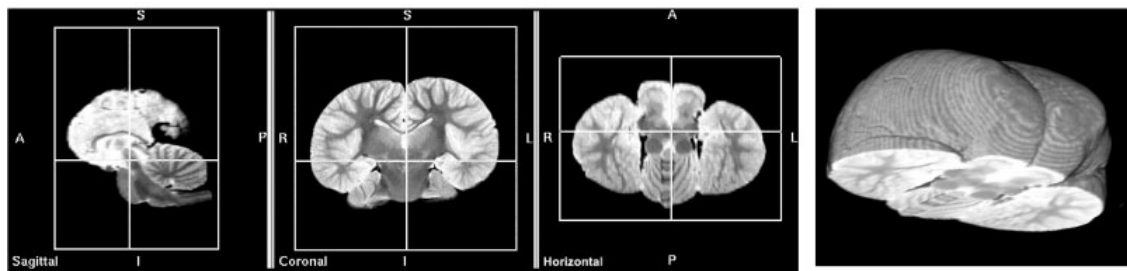
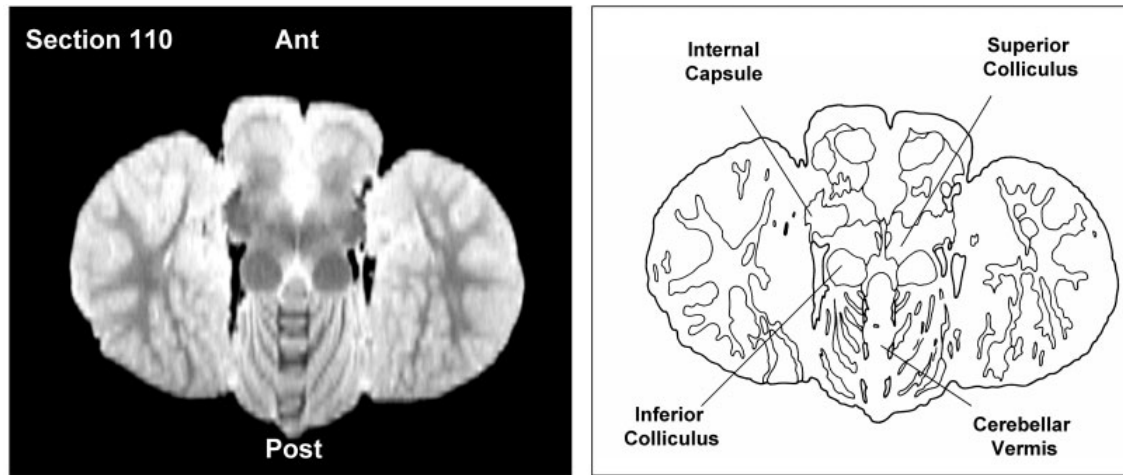


Figure 16

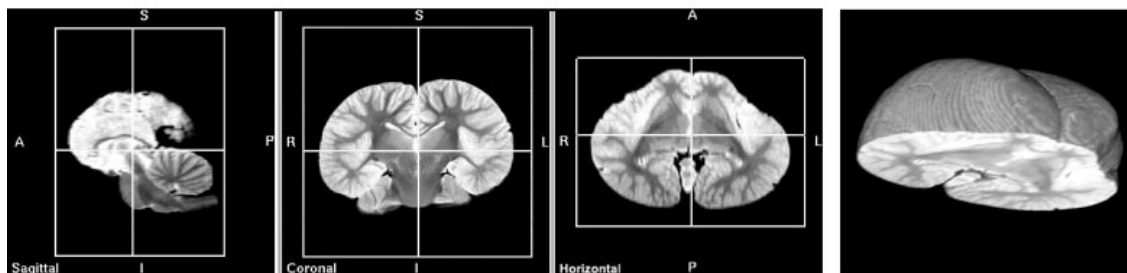
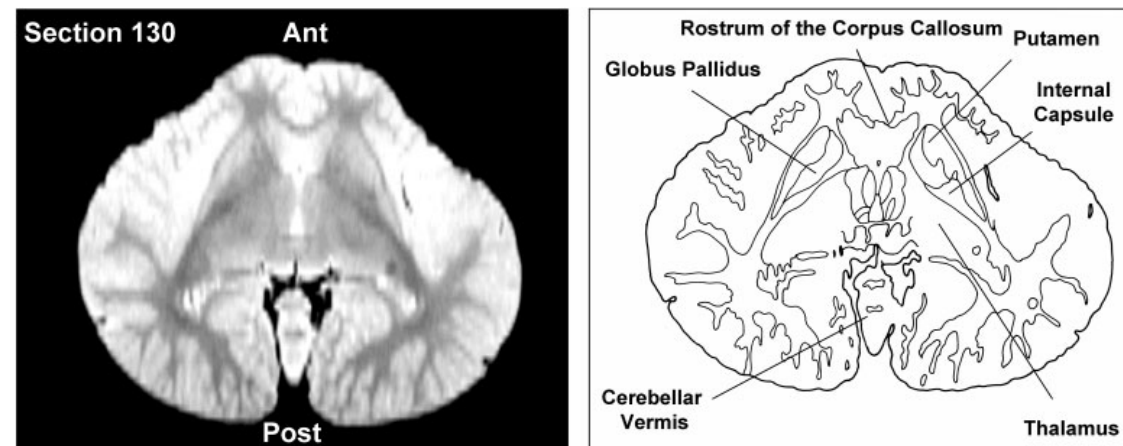


Figure 17

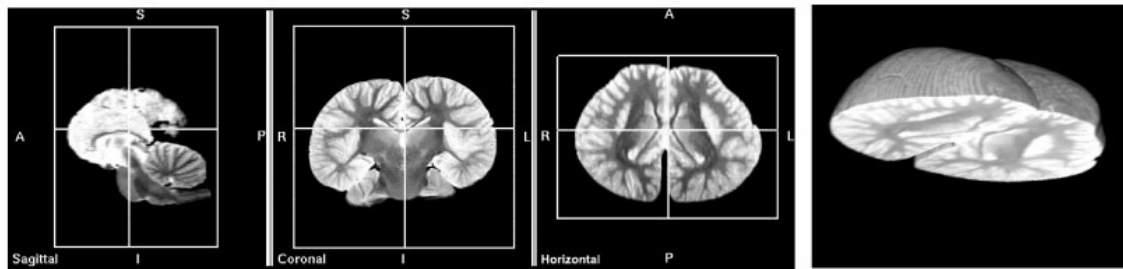
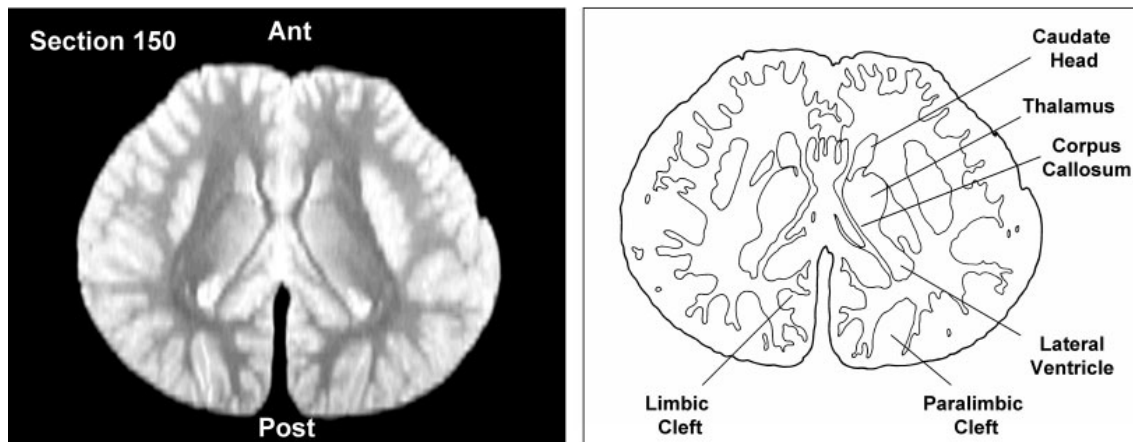


Figure 18

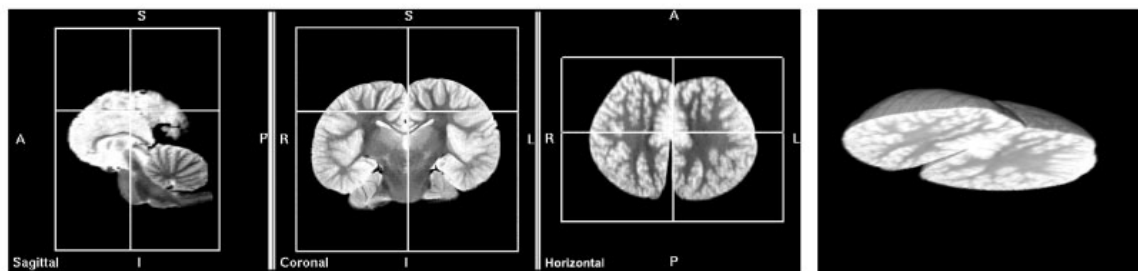
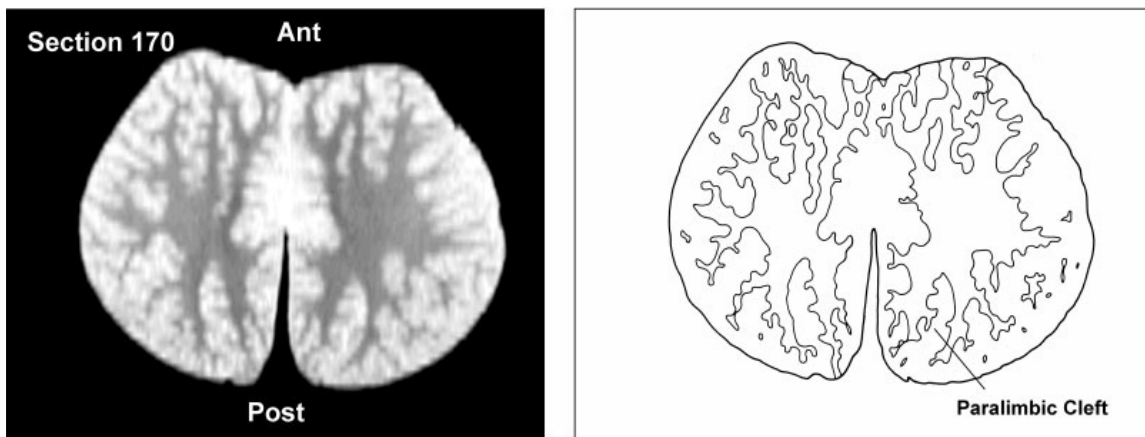
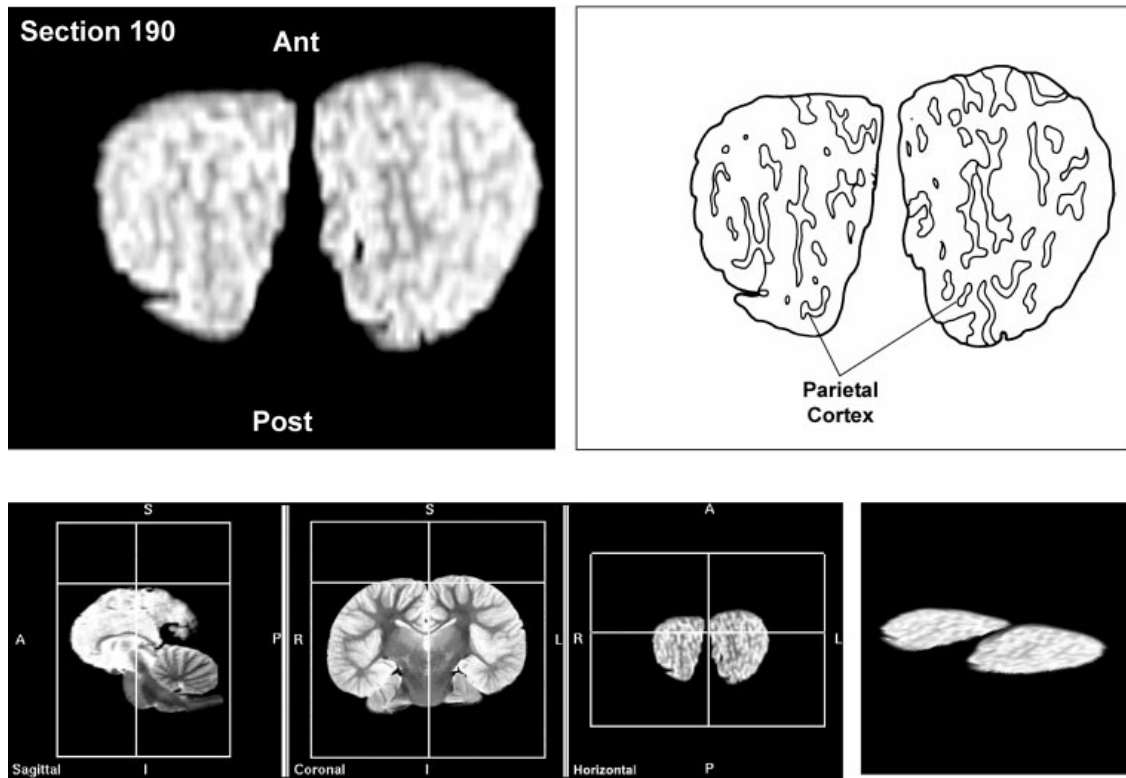


Figure 19



Comparison with fetal common dolphin brain.

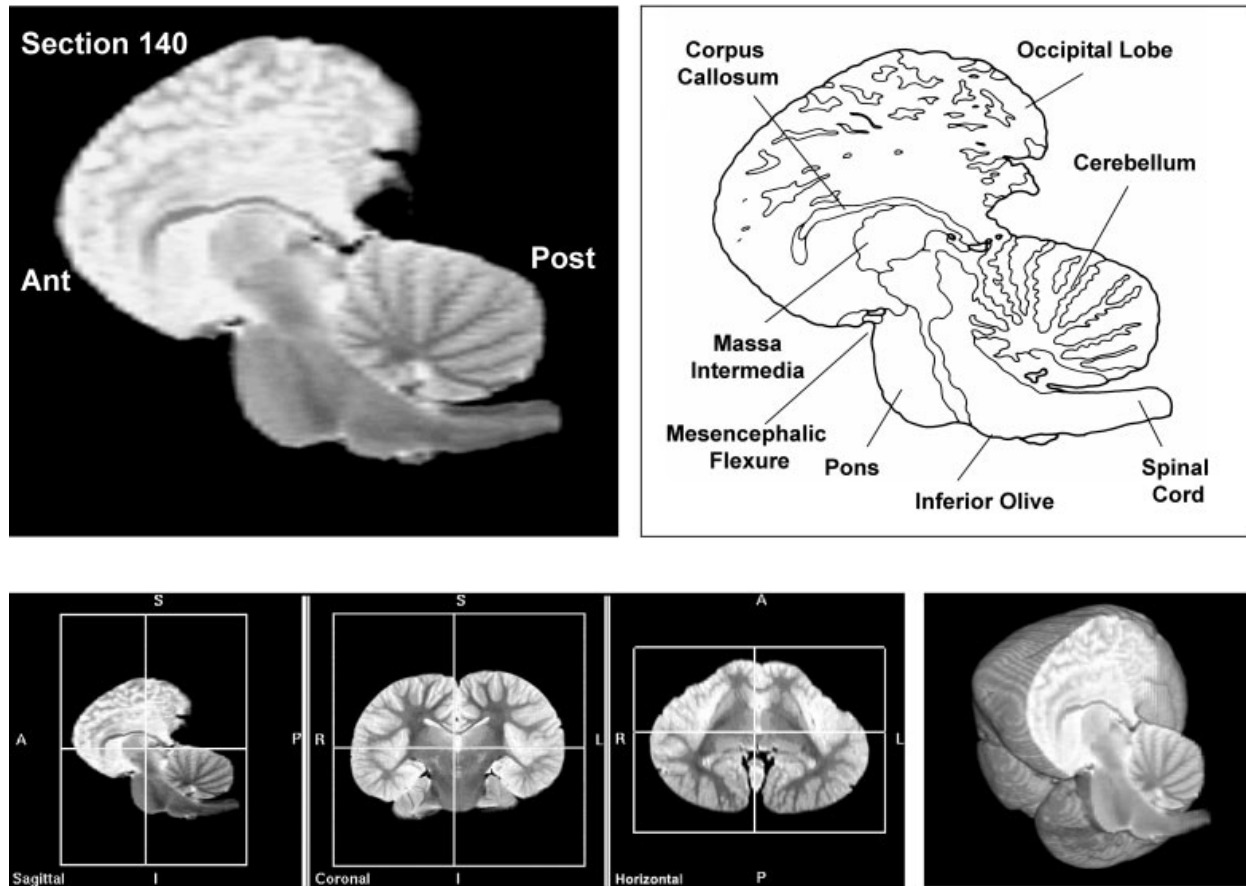
When compared with the fetal common dolphin brain (Marino et al., 2001a), the adult common dolphin brain appears very similar at the gross morphological level. One of the more obvious differences is that the adult brain does not possess olfactory bulbs. There was some suggestion of the presence of regressed olfactory bulbs in the fetal brain (Marino et al., 2001a). The three-tiered pattern of cortical clefts that is evident in the adult brain was shown to be present in the late fetal stage as well. Proportions of various structures, such as the colliculi, cerebellum, and corpus callosum, were also shown to be similar to the adult proportions in the fetal brain (Marino et al., 2001a). The lateral position of the cerebral peduncle along the ventral midbrain is also evident in the fetal brain.

DISCUSSION AND CONCLUSIONS

This work presents the first series of MRI-based anatomically-labeled sectioned images of the brain of the common dolphin. Like our previous MRI-based studies of the brains of the adult beluga whale, adult bottlenose dolphin, and the fetal common dolphin, the present study reveals the usefulness of imaging-based analyses of postmortem brain tissue in cetaceans. These images allow the distinctive features of the common dolphin brain to be visualized from various orientations by preserving the gross morphological and internal structure of the specimen. The brain of the common dolphin is characterized by morphological trends similar to those found in other cetaceans (Morgane et al., 1980) and appears very similar to the bottlenose dolphin brain. This neuroanatomical resemblance is as expected, given the close phylogenetic relationship of the common dolphin to the bottlenose dolphin (Milinkovitch et al., 1994). Although there are differences among cetacean brains (and undoubtedly between the common

dolphin and bottlenose dolphin brain), these differences are relatively minor compared with the striking dissimilarities to brains of non-cetacean mammals. Comparisons with the fetal common dolphin brain, and the close resemblance between the two, confirm the maturity of the fetal dolphin brain.

Figures 20–28. A midline–lateral sequence of reconstructed 0.7-mm-thick “virtual” sagittal sections through the left hemisphere at 5.6-mm intervals, a labeled schematic illustration of each section, computer-generated cutaways of two orthogonal planes to the section, and a computer-generated 3D reconstruction of the whole brain showing a cutaway of each section.



The present work and similar studies are critical for establishing the neurobiological basis of differences in cognition and behavior across cetaceans, as well as instances of cognitive convergence between cetaceans and other mammals. For instance, a number of cetacean species within the Delphinid family, including the common dolphin, share several behavioral and social characteristics with great apes and humans (Marino, 2002). Recently, Reiss and Marino (2001) showed that the bottlenose dolphin, a close relative of the common dolphin, is capable of mirror self-recognition, a cognitive phenomenon heretofore considered unique to great apes and humans. One of the major hypotheses concerning self-recognition ability in primates is that this capacity is related to the large frontal lobes of great apes and humans (Keenan et al., 2000; Stuss et al., 2001). However, cetaceans do not have well-developed frontal lobes; instead they possess highly elaborated parietal and temporal regions. The demonstration of mirror self-recognition in dolphins compels us to identify the analogous brain structures in bottlenose dolphins that underlie self-recognition. Given the close similarities between the bottlenose dolphin and common dolphin brains, it would not be surprising if the common dolphin was also capable of mirror self-recognition.

Figure 21

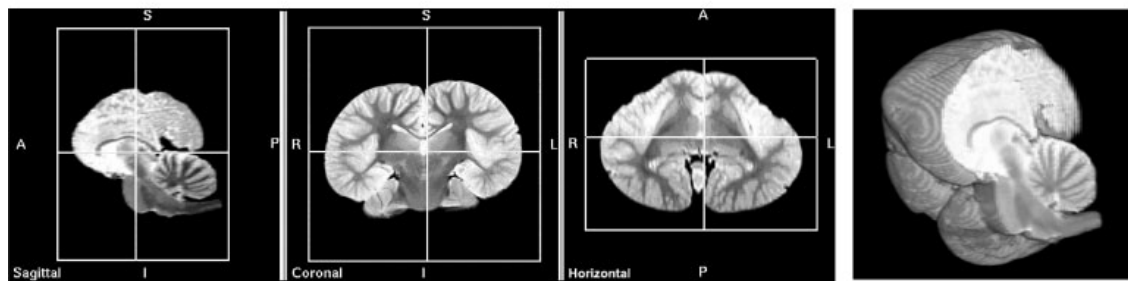
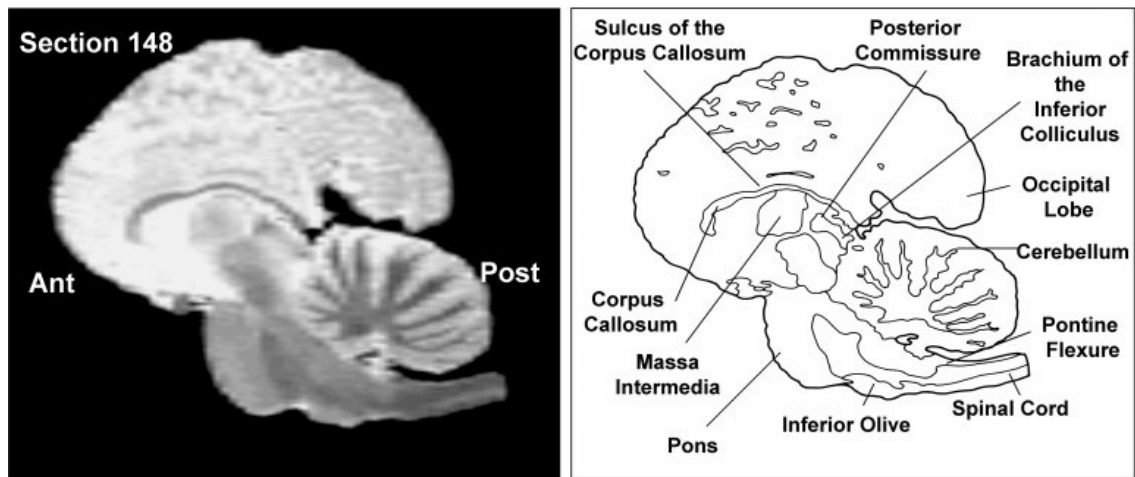


Figure 22

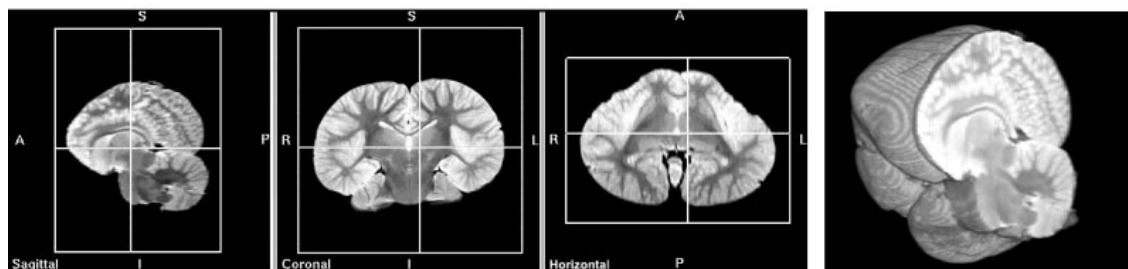
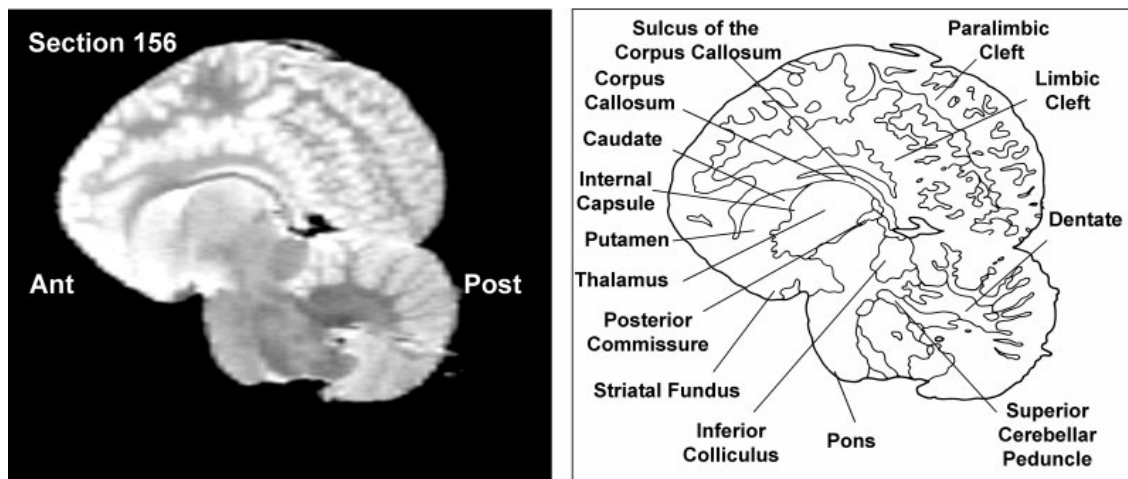


Figure 23

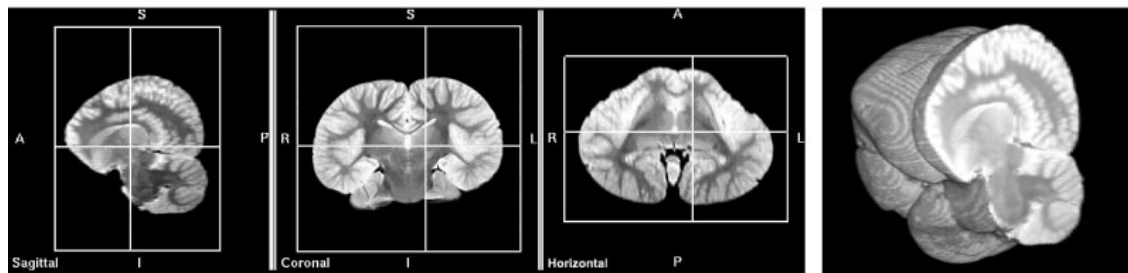
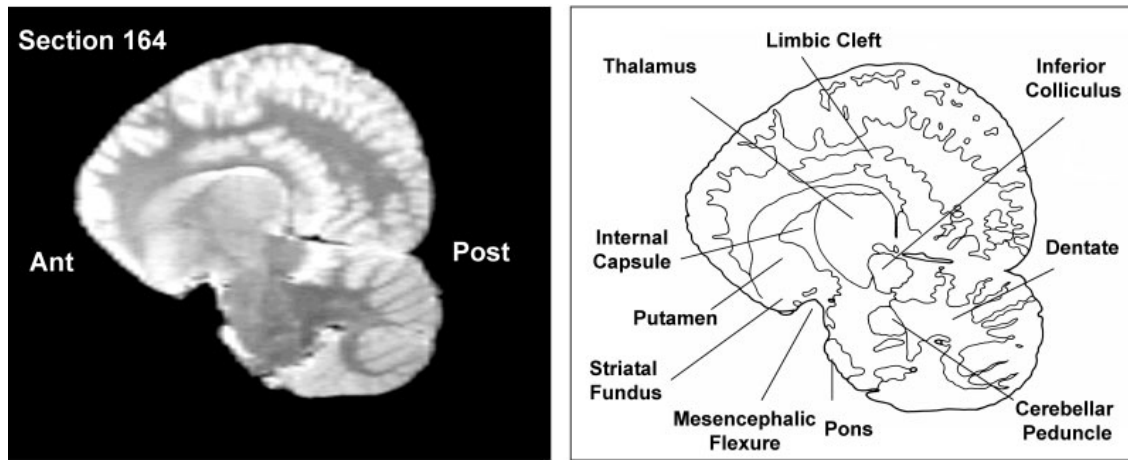


Figure 24

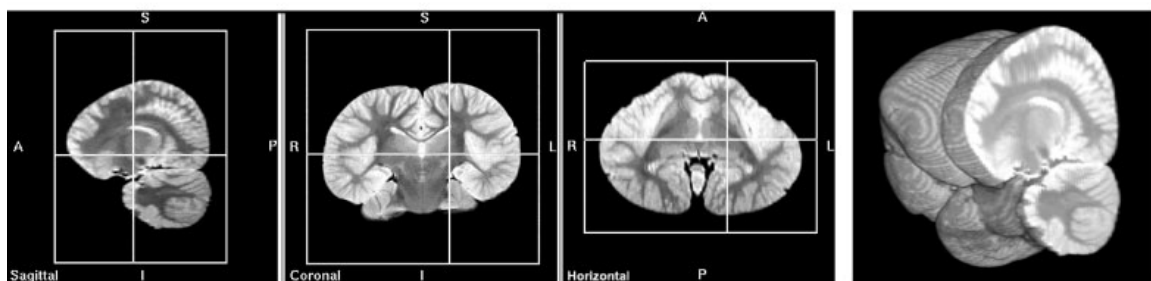
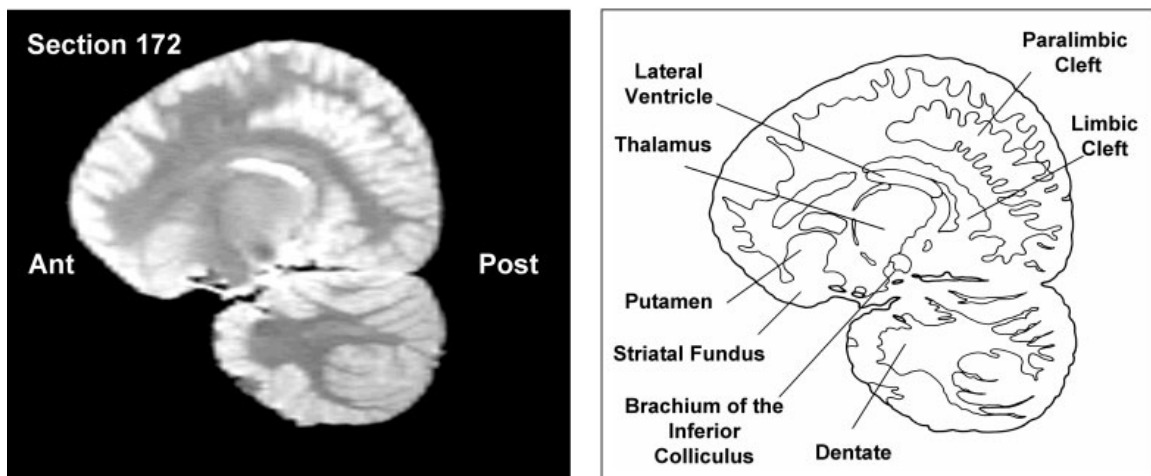


Figure 25

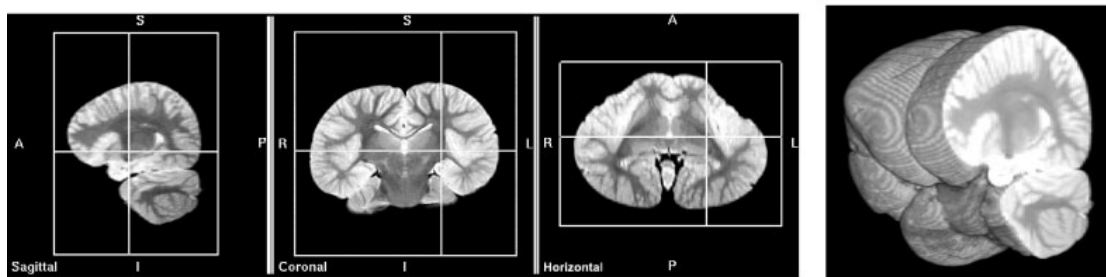
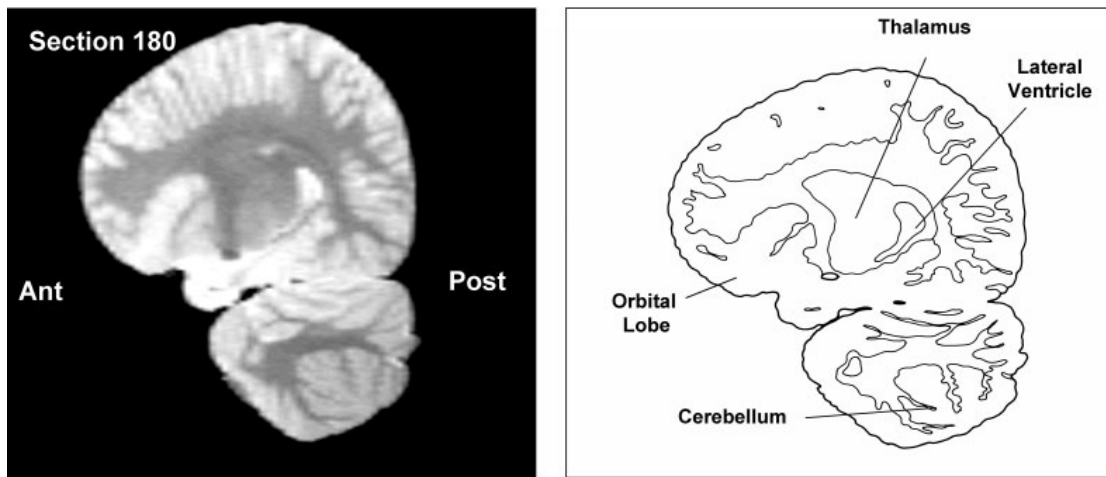


Figure 26

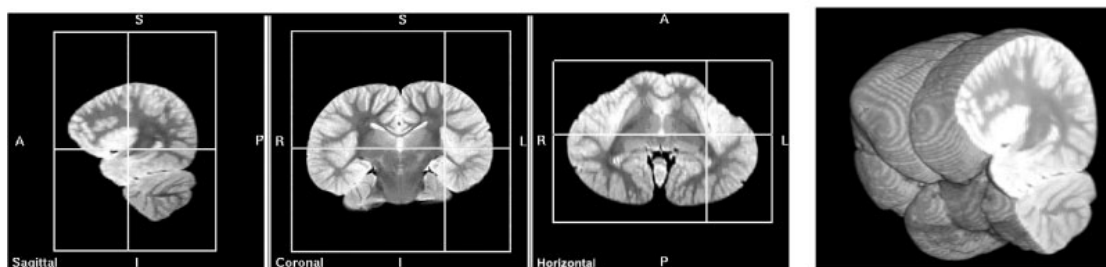
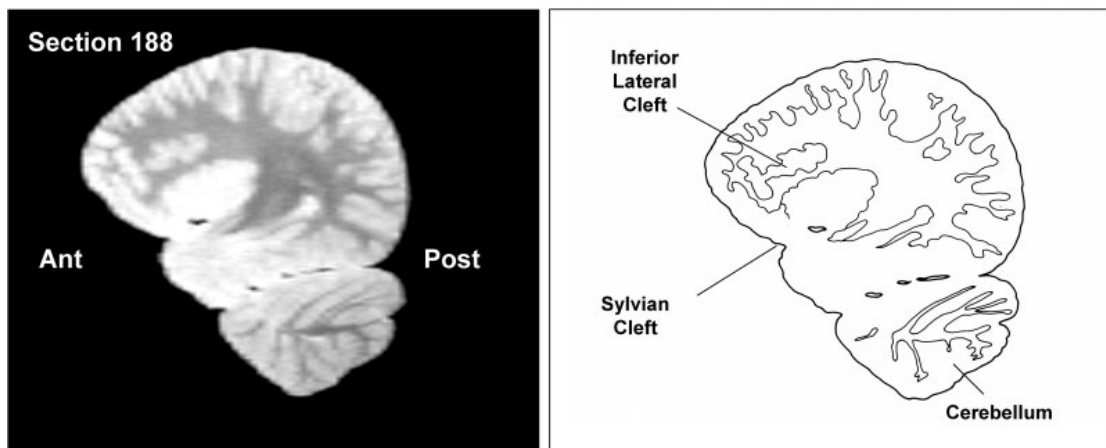


Figure 27

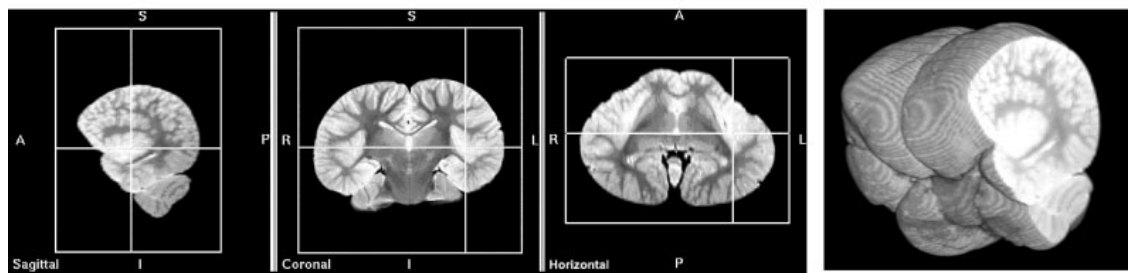
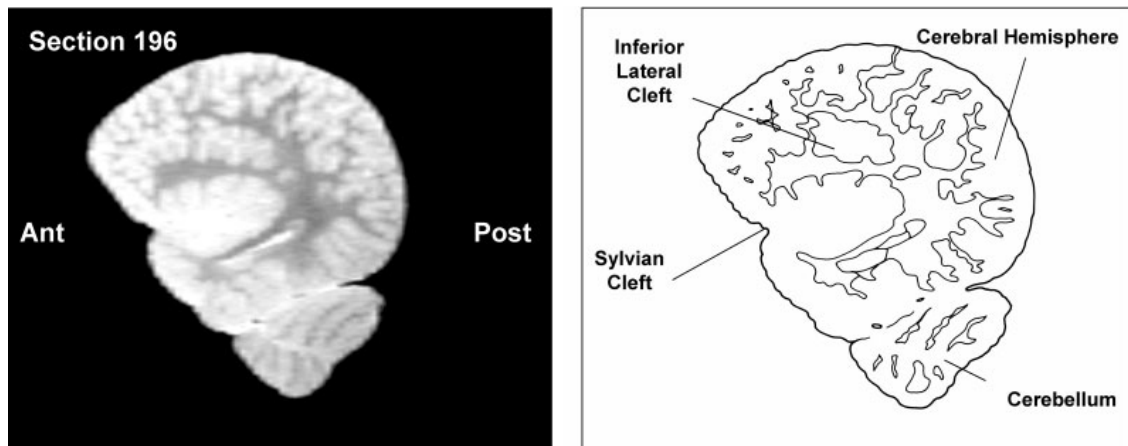
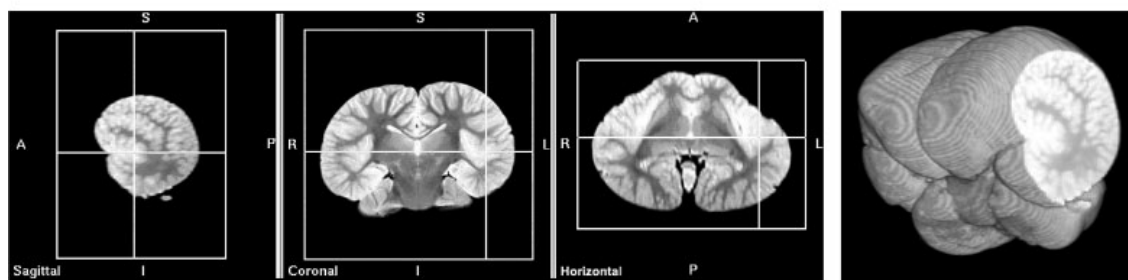
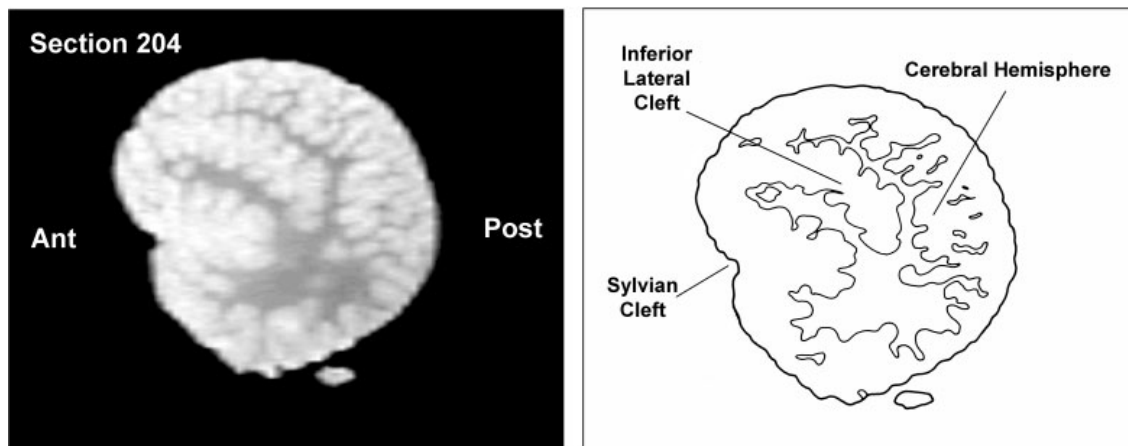


Figure 28



Studies such as the present one are crucial for forming hypotheses about which structures or features of the dolphin brain, e.g., parietal and temporal lobe elaboration, serve analogous functions to those in primate brains. These kinds of comparisons will enable us to better understand both the differences and the similarities in brain-behavior relationships between cetaceans and other taxa.

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